GYNANDROMORPHS OF *MEGACHILE ROTUNDATA* (FAB.) (HYMENOPTERA: MEGACHILIDAE)[1,2]

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ABSTRACT: Two gynandromorphs of *Megachile rotundata* (Fab.) are described. One was a bilateral specimen and homologies of structures of the male and female external genitalia were determined.

Gynandromorphs are abnormal individuals exhibiting both male and female characteristics. Although bilateral gynandromorphs (that is, individuals with one side of the body male and the other female) are most easily and commonly recognized, specimens showing anterior-posterior differences or a mosaic of sexual characteristics also occur.

Gynandromorphic individuals have been reported for a number of insects and related organisms including grasshoppers (Ritchie 1978), moths and butterflies (Manley 1971, Schmid 1973, Riotte 1978), mosquitoes (Grimstad and DeFoliart 1974, Huang 1974, Mason 1980), black flies (Dang and Peterson 1979), wasps (Cooper 1959, Greb 1933, Whiting et al. 1934, Wilson and Woolcock 1960), bees (Ruttner and Mackensen 1952, Gordh and Gulmahamad 1975) and spiders (Roberts and Parker 1973). These individuals probably also occur in other groups. Various mechanisms have been proposed to explain this phenomenon including those by Greb (1933), Rothenbuhler et al. (1951) and Ruttner and Mackensen (1952). Wigglesworth (1972) presents a short discussion of the mechanisms leading to gynandromorphic individuals.

In the Pacific Northwest, farmers maintain large numbers of the alfalfa leafcutting bee, *Megachile rotundata* (Fab.), to provide pollination for alfalfa seed production. Because of its economic importance, a vigorous research project concerning the alfalfa leafcutter has been underway in Washington State since about 1961 (Klostermeyer 1964, Johansen and Eves 1966, Johansen and Klostermeyer 1967, Johansen et al. 1963). However, in the handling and examining of thousands of bees each year, only three gynandromorphic individuals have been discovered. While this indicates that these individuals rarely occur, few data are available for consideration. However, only one specimen was found among 2,657

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individually examined females last year (1981, pesticide testing) for a ratio of 1:2,656. This compares to 1:10,000 for gynandromorphs in scolioid wasps, genus *Myzinum* (Krombein 1949) and 1:3800 for gynandromorphs in pompilids (Evans 1951). The first gynandromorph was a bilateral specimen, but unfortunately only a cursorial study, which did not include an examination of the external genitalia, was conducted (Gerber and Akre 1969). Since then, two additional gynandromorphs have been found. The purpose of this paper is to describe these two individuals and to relate the morphology of one of them to the evolution of insect genitalia (Smith 1969).

Specimen 1

A "gynandromorph" was collected 28 July 1972 as it emerged from a group of prepupae maintained in the laboratory at the Irrigated Agriculture Research and Extension Center, Washington State University, Prosser, WA. This specimen was placed in alcohol until examined 10 July 1981.

The specimen was thoroughly examined externally, and was dissected to examine the reproductive tract. Although not well preserved internally, it contained two definite ovaries. The external genitalia were female but were somewhat abnormal as only a single valvula 2 (gonapophysis 9) was present. All other sclerites were present and shaped normally (an illustrated description of normal genitalia is presented in Gerber and Akre 1969). Externally the specimen lacked scopal bristles from sterna 3-6 on the left side of the gaster, otherwise it was a typical female in coloration and morphology.

Specimen 2

The second specimen emerged 27 April 1981 from peeled cells produced in the Yakima Valley, Washington. These cells, containing prepupae of *Megachile,* were incubated in the laboratory, and emerging adults were being used in various experiments. Examination showed the specimen to be a bilateral gynandromorph with one side male, the other female (Figs. 1 and 2). It was killed 29 April and injected with Kahle's solution so the reproductive tract was preserved.

Head: The left side of the head was typically male with long, golden-yellow hair. The antenna had 13 segments. The right side of the head was covered with short, white hairs, and the antenna was 12 segmented; typical female characterisitics. In addition, the right mandible was female with 4 sharply pointed teeth, while the left was typically male with 2 blunt teeth, and a medially-facing, sharp, subapical tooth (Gerber and Akre 1969). The

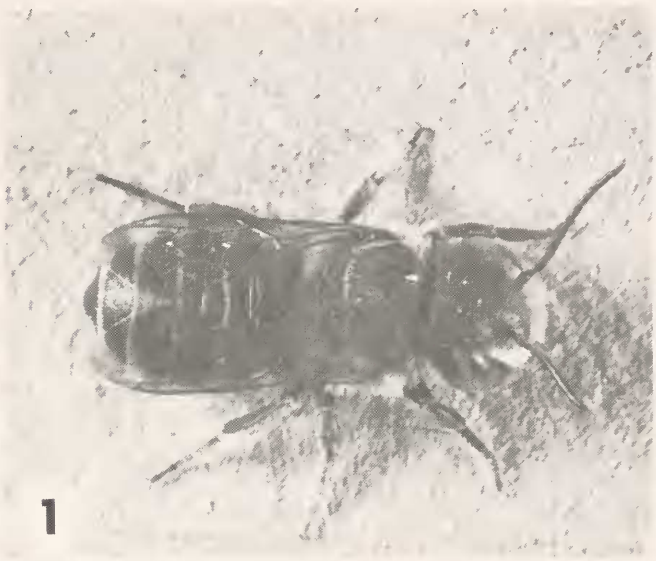

Fig. 1. Gynandromorph of *M. rotundata.* The left (male) antenna is longer. Fig. 2. Ventral view of specimen showing scopa (female character) on left side of gaster.

right, lateral ocellus was slightly displaced to one side (.52 mm) from the median ocellus compared to the other (.31 mm). The entire labio-maxillary complex was distinctly offset and originated on the female side of the head. The glossa (tongue) was hairy (Fig. 3) indicating these mouth parts were entirely female. Male glossae are always bare.

Thorax: The male/female sides of the thorax were reversed from that of the head. The right side (male) was covered with long, golden hair, the first coxa had a coxal tooth, and all 3 tarsi had bifid claws. The left side (female) had short, white hair, no prothoracic coxal tooth and the tarsal claws were all single (see Gerber and Akre 1969). The wings were of slightly unequal length; left front (female) 5.77 mm, the right front 6.18 mm.

Gaster: The gaster showed the most striking gynandromorphic features, especially the total absence of scopal bristles on the right side (male) (Fig. 2). The 5th sternum was normal, but the 6th was highly modified with a small sclerotized patch just lateral to the midline. A normal female has 7 externally visible sterna, the male only five, with the 6th and 7th lying underneath (dorsal to) the fifth. Thus, when these two unequal "halves" were fused together, displacement occurred. In this specimen, the 6th sternum on the male side was mostly membrane, with a small sclerotized patch, the 7th was probably represented only by membrane (Fig. 4).

Reproductive system: Typical females of *Megachile rotundata* have ovaries consisting of 6 ovarioles, 3 per side, while males have the testes fused into a single unit (Figs. 5a, b). Posteroventrally to the testes are paired dilations, the seminal vesicles, and the tract continues as small tubes, the paired vas deferens.

The gynandromorph had one ovariole on the left (female) side, containing at least 3 well defined oocytes/nurse cells (Fig. 5c). Basal to the oocytes, the oviduct continued as a single tube into the ovipositor. Issuing from somewhere near the base (connection inadvertently broken) was a single accessory gland, the Dufour's gland. In normal females the duct from the Dufour's gland and the duct from the poison gland reservoir continue into the sting bulb. The reproductive tract was not as well developed on the right (male) side. The most discernible structure was the nearly spherical seminal vesicle. The testis was represented by a short, slightly coiled tube issuing from the apical end of this dilation. A single vas deferens connected the tract to the base of the male genitalia (Fig. 5c). A small sheet of tissue was adnate to both the vas deferens and to the lateral oviduct, otherwise they were totally separate.

Genitalia: Normal Genitalia: Smith (1969, see also Smith 1970, Matsuda 1976), in discussing the evolution of insect genitalia, proposed that these appendages are primarily limb derivatives, and presented evidence indicating that mouth parts, thoracic legs, abdominal prolegs, and

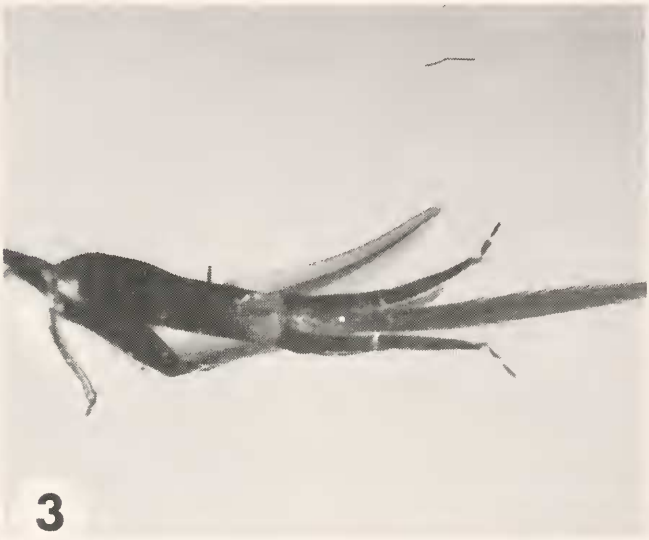

Fig. 3. The glossa was hairy indicating the maxillary/labial complex was female. **Fig. 4.** Terminal segments of gaster showing genitalia. 5S=5th sternum.

genital appendages are homologous. [This topic has been somewhat controversial, particularly in regard to Hymenoptera genitalia, and has been subject to various interpretations (Michener 1944, Matsuda 1958)]. Hymenoptera retain a primitive condition for the ovipositor (female), and gonocoxites 8 (valvifer 1) give rise to the 1st pair of gonapophyses (valvulae I), while gonocoxites 9 (valvifer 2) gives rise to the 2nd pair of gonapophyses (valvulae II) anteriorly, and a pair of gonostyli (valvulae III, sting sheath) posteriorly. Gonapophyses 9 (valvulae II, stylet in honey bee sting apparatus terminology) are fused into an elongated trough which contains gonapophyses I (valvulae I, lancets of honey bee). Thus, the sting is a fairly rigid structure composed of gonapophyses 8 and 9; the sting sheath (gonostyli 9) is folded up out of the way when the sting is used (Snodgrass 1956, see also Akre et al. 1981).

Conversely, the male has lost all appendages of segment 8 (no gonapophyses 8), and gonocoxites 9 give rise to a pair of gonapophyses (penis valves). Gonostyli 9 (sting sheath of female) are modified into claspers, the gonoclaspers or gonoforceps. The genital appendages are not rigidly articulated to tergite 9 as in the female which gives the phallus maximal flexibility in contrast to the fairly rigid sting.

Gynandromorph: Female: Gonapophyses 8 and 9 (valvulae I and II) originated on the female side, but extended across the male (right) side of the specimen (Fig. 4). The 7th tergum was removed exposing hemitergite 8 (identified by a spiracle in the posterior margin) which overlapped the 9th tergite (Figs. 6b,d). Gonocoxites 8 (valvifer I) and 9 (valvifer II) were shaped normally. Gonapophyses 8 and 9, however, were somewhat twisted near the distal end. These would typically fuse with the corresponding pair from the other side in a normal individual, but because these corresponding structures were lacking, the gonapophyses extended out over the male side.

Male: This extension of the female genitalia over the male side displaced the male-side genitalia and caused them to rotate ca. 180° (Fig. 6a). They appear in Fig. 4 in a position that suggests they also originated on the female side. However, dissection clearly shows that these structures originated on the male side, but the partial fusion of the unequal sclerites (♂, ♀) caused them to rotate into position. The 7th tergum of the male was mostly membrane (Fig. 6c). Hemitergite 8 (identified by the spiracle) was overlapped by 7, and had a narrow sclerotic bar connecting it to hemitergite 8 on the female side (Fig. 6e). The eighth sternum was somewhat modified, but still bore a short process from the proximal end. As in normal males, the 9th sternum was represented by a small sclerite lying dorsolateral to the 8th (Figs. 6c, e). The remaining genital appendages were rotated to a position dorsolateral to the 8th and 9th sterna. Gonostylus 9 (valvula III of female, gonoforceps) was easily identified by its shape (Figs. 6b, d). A small sclerite and a sclerotic bar at the base of gonostylus 9 represented the gonocoxite/

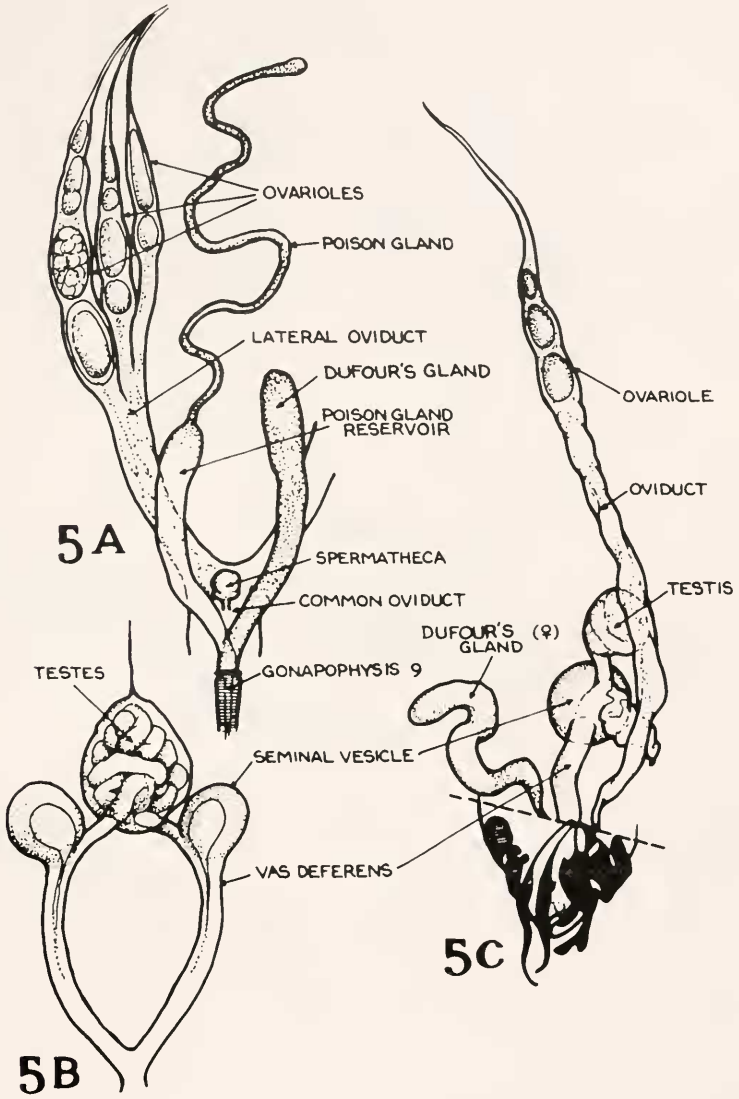

Fig. 5. Internal reproductive systems of *M. rotundata*. A. normal female. B. normal male. C. gynandromorph.

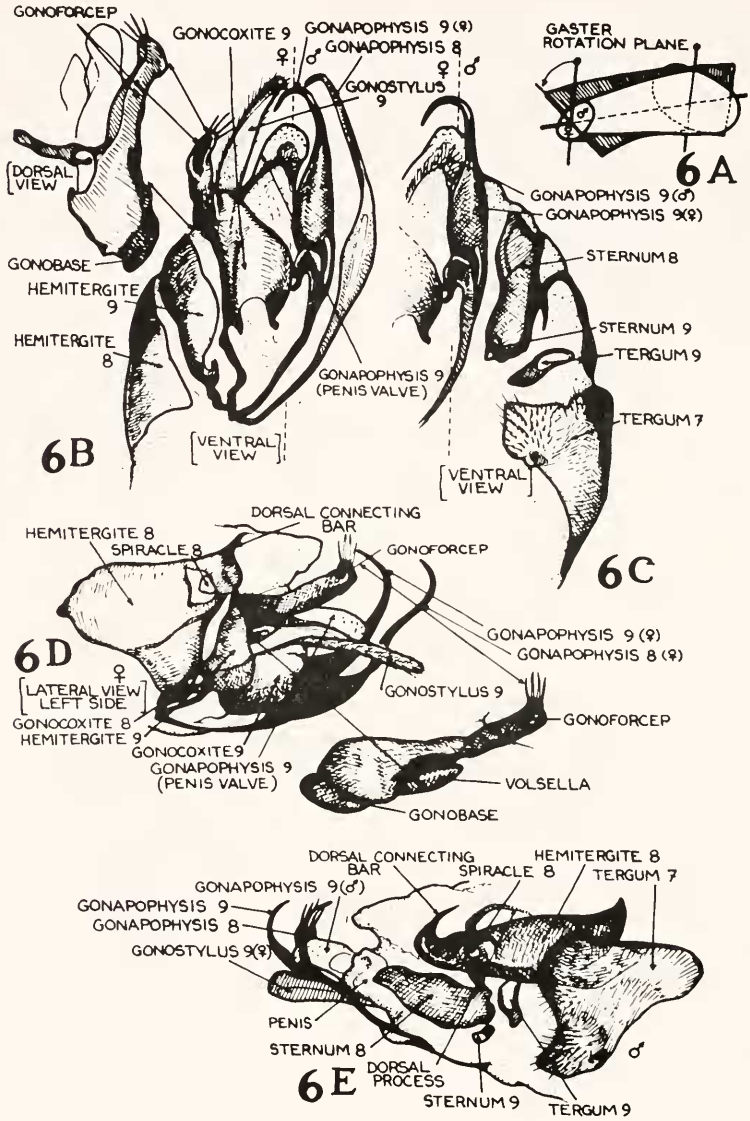

Fig. 6. External genitalia of gynandromorph. A. diagram indicating the longitudinal twist of the gaster. B. Ventral view of female half. C. Ventral view of male half. D. Lateral view of female half. E. Lateral view of male half.

gonobase (Gerber and Akre 1969) that forms a solid arch at the base of the genitalia in normal males (Fig. 6d). Medially to gonostylus 9 was gonapophysis 9, the penis valve (Figs. 6d, e). A membranous structure medial to this structure probably represented a malformed, partial penis (Gerber and Akre 1969, Fig. 6e).

Discussion

This bilateral gynandromorph offered a unique opportunity to evaluate Smith's (1969) hypothesis on male genitalic origin as it pertains to Hymenoptera. Our examination of this specimen supports Smith's interpretation. A summary chart follows:

	Gynandromorph	
	♀ Side	♂ Side
gonocoxite 8 (valvifer I)	present	lost in pterygotes (represented by partial 8th sternum)
gonapophysis 8 (valvula I)	present (twisted)	lost
gonocoxite 9 (valvifer II)	normal shape	gonocoxite 9
gonapophysis 9 (valvula II)	present (twisted)	gonapophysis 9 (penis valve)
gonostylus 9 (valvula III)	present (sting sheath)	gonostylus 9 (gonoforcep)

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